

A NEW PORCUPINE FROM THE MIDDLE PLEISTOCENE OF THE ANZA-BORREGO DESERT OF CALIFORNIA

With notes on mastication in *Coendou* and *Erethizon*

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ABSTRACT: A new species of *Coendou* is described from the Middle Pleistocene of the Anza-Borrego Desert.

The genera *Coendou* and *Erethizon* are distinguished from one another by means of inferred differences in mastication, and it is postulated that *Coendou* is ancestral to *Erethizon*.

INTRODUCTION

A large and diversified collection of fossil vertebrates has been obtained from the highly fossiliferous badlands of the Vallecito Creek Valley and Fish Creek Wash areas of the Anza-Borrego Desert in the western Imperial Valley of Southern California. This collection has resulted from the extensive field operations in that area conducted by the Vertebrate Paleontology Section of the Los Angeles County Museum of Natural History under the direction of Theodore Downs.

The sediments comprise the Palm Springs formation (Woodring 1931; Dibblee 1954) and consist of mudstones, siltstones, and sandstones which are occasionally cross-bedded. That part of the formation from which the above collection was made is exposed on the south limb of a west-plunging anticline (Woodard 1963), and dips 24 to 26 degrees to the south. It is in continuous sequence through more than 10,000 feet. The porcupine specimens described herein have been collected from within the upper 3,000 feet of this section, which is Irvingtonian (Middle Pleistocene) in age (Downs 1957; White and Downs 1961; Howard 1963; White 1964).

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SPECIMENS EXAMINED

An estimated 400 specimens of *Erethizon* and 25 *Coendou* were examined. Only the specimens that were measured are listed here with their museum numbers.

Coendou mexicanus: MVZ 116815, 116817, 124088; USNM (Mammalogy) 296308, 298915, 303135, 303277, 306980, 324110, 335666; skeletons: 240269, 240312, 257008, 257364; KUM (Mammalogy) 18190, 18191, 19888, 19889, 24489, 24490, 24491, 32180, 93790, 93791, 93793, 93794; UMM *Coendou* sp. V47106; ?*Coendou brachynathum* USNM (Vertebrate Paleontology) 13684.

Erethizon dorsatum: MVZ 4052, 4508, 4510, 4467, 4496, 51382, 40874, 42073, 42077, 42078, 42079, 46906, 53702, 53263, 58496, 67689, 68707, 68708, 74292, 79588, 84036, 84969, 84970, 87862, 89556, 106164; USNM (Mammalogy): skeletons: 49420, 90476, 192546, 241005; (Vertebrate Paleontology): 7668-7673, 7996, 8128, 8130, 8134, 8174.

A number of specimens of porcupines referable to the genus *Coendou*, to which belong the prehensile-tailed porcupines of the rain forests of Central and South America, have been collected in the above-mentioned geological section, and differ morphologically from known species of the genus to such a degree that they are assigned to a new species.

***Coendou stirtoni* new species**

Type: LACM 17633, fragmentary palate with LP⁴-M¹, RP⁴ (partial), M¹ and M² (Fig. 1).

Type Locality: LACM 1428, Arroyo Tapiado, Badlands in Anza-Borrego Desert State Park, San Diego County, California.

Horizon: Approximately 2900 feet stratigraphically below top of the Palm Spring formation in the Tapiado member of the formation (Woodard 1963).



Fig. 1A

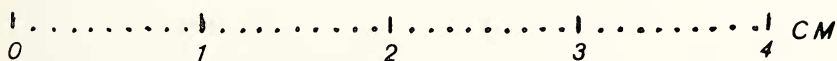


Fig. 1B

Figure 1. *Coendou stirtoni* n. sp., LACM 17633, type specimen, stereophotograph of the palate (A); ventral view of palate (B).

Referred Specimens: LACM 6136, a partial skeleton with palate and medial part of RM², ventral portion of rostrum, fragmentary left mandible with broken teeth, sacrum and 12 caudal vertebrae, proximal end of left radius, broken proximal right ulna, partial ischium with part of acetabulum, proximal end of left femur; 6210 and 6210A, two fragmentary left mandibles with broken teeth; 4325, a partial skeleton lacking skull parts, but with distal part of right humerus, right radius and ulna with distal epiphyses missing, proximal portion of left ulna, right femur with distal epiphysis missing, left astragalus, right calcaneus, left cuboideum, and seven phalangeal elements.

Diagnosis: Erethizontid with width of palate between right and left P⁴'s at least 40 per cent of width of palate between M³'s in adults; width of P⁴ approximately the same as width of M¹; adults as large as a large adult *Erethizon*, and far larger than any species of living *Coendou*.

Description: The occlusal pattern of the cheek teeth in *Coendou stirtoni* is essentially the same as in other species of *Coendou* and in *Erethizon*. The large size of the teeth in the new species tends to cause the occlusal patterns of the cheek teeth to resemble those in *Erethizon* more than those in *Coendou*; however the living species of the latter genus have teeth that are markedly smaller in size than in *Erethizon* and in the larger, extinct species of *Coendou*. This marked difference in size may account for the dissimilarity of tooth pattern. P⁴ is as wide as M¹ in the new species and in all specimens of living *Coendou* examined, while in all specimens of *Erethizon* P⁴ is markedly larger than M¹. In juvenile specimens of *Erethizon*, DM⁴ is as wide as M¹, and DM⁴ and P⁴ resemble one another morphologically in *Coendou* and *Erethizon*. In the type specimen of *C. stirtoni*, the broken roots of DM⁴ are visible on the sides of the alveolus of P⁴.

Although mandibular cheek teeth are unknown for *C. stirtoni*, P₄ in *Erethizon* is, on the whole, larger than M₁ while in *Coendou* the two teeth tend to be subequal in size. The relationship between P⁴ and M¹ is more consistent than that between P₄ and M₁ (compare Figs. 4 and 5). The latter exhibits considerable variation and is of limited taxonomic use (Hibbard and Mooser 1963). Only in rare cases when P₄ is markedly larger than M₁ can *Erethizon* be identified by this character.

In mandibles LACM 6210A and 6136, the base of the ascending ramus indicates that it slanted posteriad, permitting the cheek teeth to be visible from the side (Hibbard and Mooser *ibid.*), as in other species of *Coendou*.

In mandibles LACM 6210 and 6210A the proximal, approximately three-fourths of the inflected angular process is present and is as in *Coendou*, wherein it is subparallel to a midline separating the mandibles, and not inflected to the degree it is in *Erethizon*. The greater inflection seems to reflect the marked divergence posteriad of the cheek teeth in the latter genus.

Unfortunately, only four skeletons each of *Coendou* and *Erethizon* were

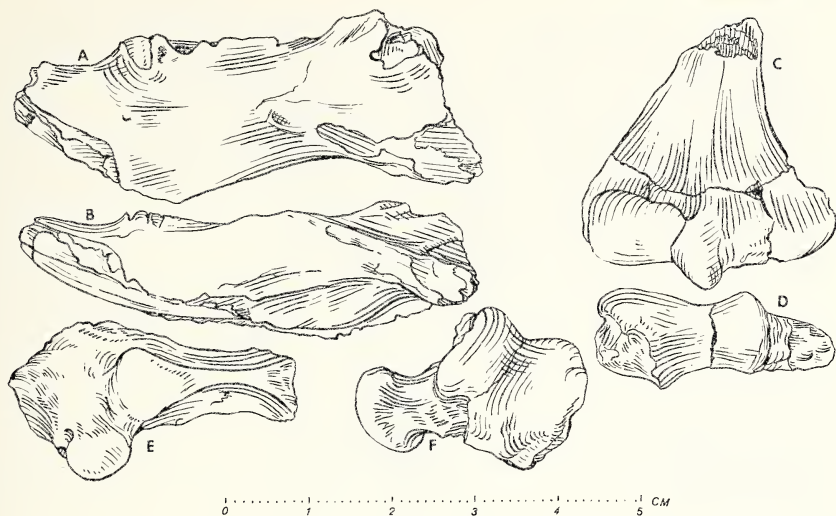


Figure 2. *Coendou stirtoni* n. sp. Lateral (A) and ventral (B) views of left mandible, LACM 6210A; anterior (C) and distal (D) views of right humerus; dorsal view of left astragalus (E), LACM 4325; and dorsal view of right calcaneus (F), LACM 4325.

available for comparison with two partial skeletons of *C. stirtoni*. *C. stirtoni* resembles both genera in most observable skeletal characters but differs in the following:

The medial epicondyle of the humerus (Fig. 2 C and D) in *Coendou* and in *C. stirtoni* is oriented laterad, whereas in *Erethizon* it extends posteriad. Since the digital flexor muscles have origin mostly on the medial epicondyle, one is tempted to relate this difference to the known difference in habitus existing between living *Coendou* and *Erethizon*. More needs to be known about the functional anatomy of these forms before such conclusions can be made, however.

The proximal articular surface of the radius in specimen LACM 6136 is ovoid, similar to the condition in *Coendou*, while in *Erethizon* it is rounded. The portion of the articular facet of the acetabulum present on the ischium in specimen LACM 6136 is elongated as it is in *Coendou*, while in *Erethizon* it is rounded. The femur (Fig. 3A) in specimens 6136 and 4325 has a well-developed third trochanter as in *Erethizon*. In *Coendou* this trochanter is poorly developed (Gupta 1966). The neck of the astragalus in specimen 4325 is distinct as in *Coendou* while in *Erethizon* it is less so.

The caudal vertebrae in specimen 6136 were not found in articular position, but when they are lined up in a sand box it seems likely they did articulate. The last caudal to have a zygapophyses is the ninth. If this interpretation is

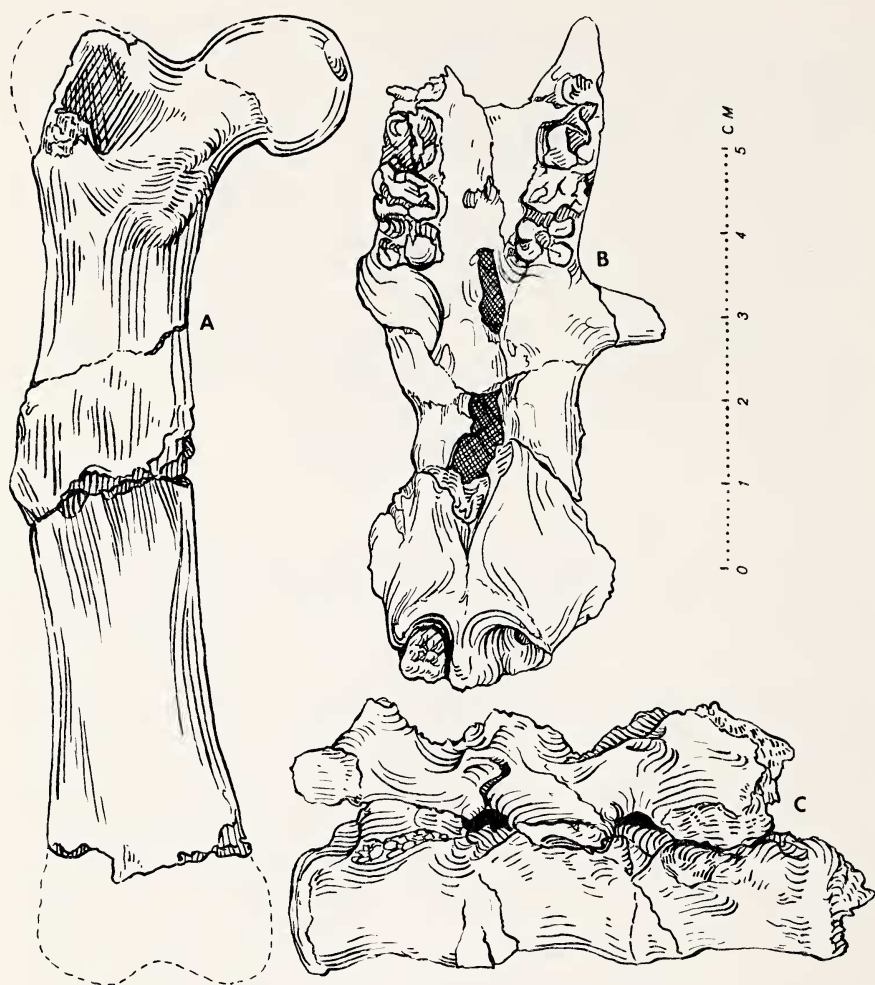


Figure 3. *Coendou stirtoni* n. sp., LACM 6136. Posterior view of left femur (A); ventral view of palate and rostrum (B); and right-lateral view of the sacrum (C).

correct, then it would seem that *C. stirtoni*, like *Erethizon*, did not have a prehensile tail. In living *Coendou* the last caudal to have zygapophyses is the eighteenth (Gupta *ibid.*).

The sacrum (Fig. 3C) in specimen 6136 consists of four fused vertebrae, the neural spines of which are unfused as in adults of living *Coendou* (Gupta *ibid.*).

Named in honor of the late R. A. Stirton.

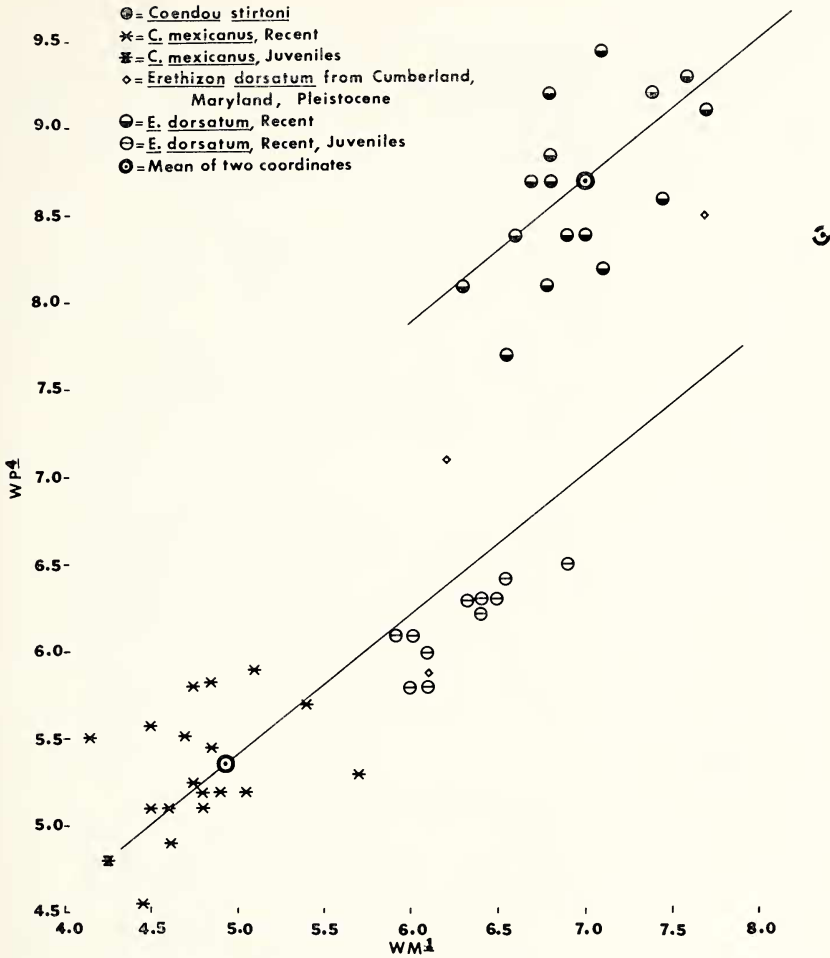


Figure 4. Scatter diagram and calculated reduced major axes (diagonal lines) modified from Imbrie (1956) for adults of *Erethizon dorsatum* and *Coendou mexicanus*. The wide separation of the two lines indicates a significant difference between the two samples.

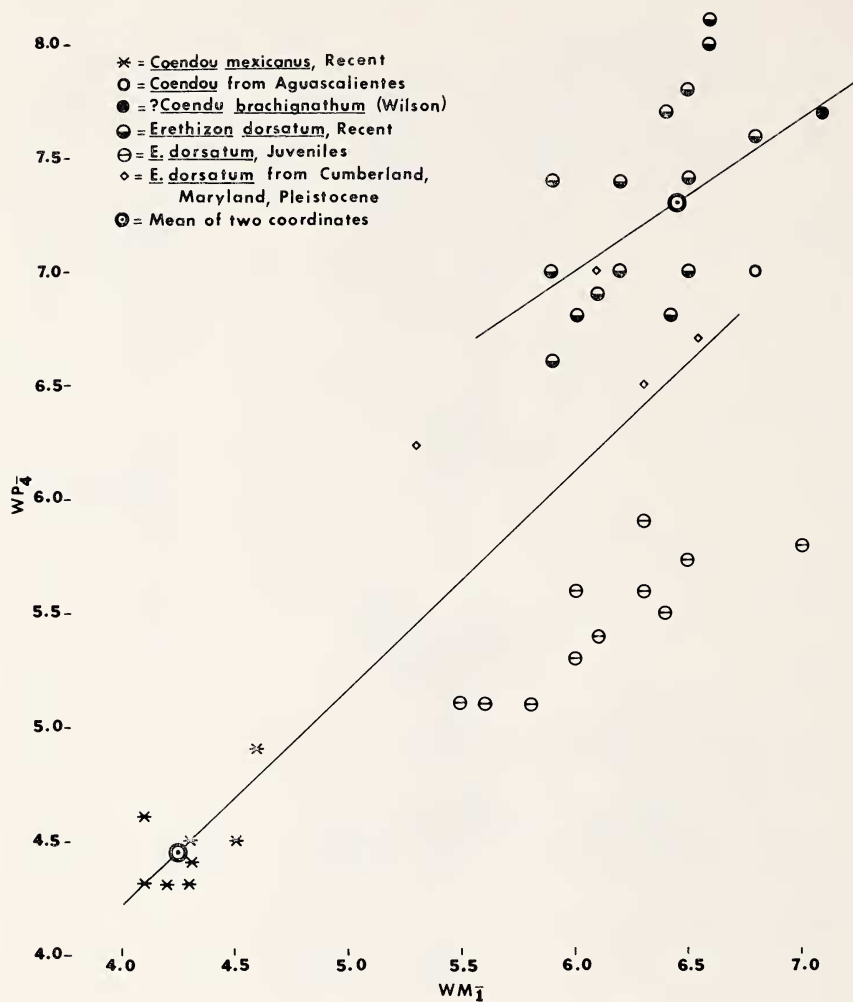


Figure 5. Scatter diagram and calculated reduced major axes (diagonal lines) for adults of *Erethizon dorsatum* and *Coendou mexicanus*. See Figure 4 for additional details.

DISCUSSION

The living species of *Coendou* are adapted to an arboreal habitus, more so than the species of *Erethizon*. The tail in the former is prehensile, while in the latter it is not. It seems likely that *C. stirtoni* had a habitus more like *Erethizon* than the living *Coendou*. The latter inference is based upon the presence of a well-developed third trochanter on the femur, on the presence of zygapophyses only up to the ninth caudal vertebra, and on the large size of *C. stirtoni*.

The degree of divergence posteriad of the upper and lower cheek teeth in adults of *Erethizon* versus the subparallel arrangement of the cheek teeth in *Coendou* (Figs. 6 and 7), seems to reflect a difference in mastication between the two genera. This functional difference can be established as follows:

1. The scratches on the enamel of the occlusal surfaces in both the upper and lower cheek teeth are oriented anteromedial and form an angle greater than 35 degrees with the longitudinal axis of the tooth rows in *Coendou* (Landry 1959). In *Erethizon* this angle is less than 30 degrees (Fig. 8).
2. The angular process of the mandible in adults of *Erethizon* is inflected medial and the posterolateral surface of the mandible is convex, while in *Coendou* and in juvenile *Erethizon* the angular processes are subparallel and the posterolateral surface of the mandible is flattened.
3. The fossa for the insertion of *M. masseter medialis pars posterior* on the side of the mandible is deeper in *Coendou* than in adults of *Erethizon*. This structure seems related to the degree of inflection of the angular process and to the degree of convexity seen in the posterolateral part of the mandible.
4. The ascending ramus of the mandible in *Coendou* slants posteriad to a greater degree than in adults of *Erethizon*.
5. In adults of *Erethizon* the projection of a line superimposed upon the longitudinal axis of the lower tooth row and bisecting the occlusal surfaces of P_4 and M_3 , passes medial to the incisor, while in *Coendou* it extends to the posteromedial surface or even laterad to the incisor (Fig. 8). This measurement makes it possible to determine if the mandibular cheek teeth converge as in adults of *Erethizon*, or are subparallel as in *Coendou* and juvenile *Erethizon*.

Juvenile specimens of *Erethizon* have subparallel cheek-tooth rows as well as all the characters mentioned above for the mandibles of *Coendou*. This suggests a pedomorphic relationship between the two genera, in that the adult condition in *Coendou* is found only in the juveniles of *Erethizon*.

In his description of mastication in *Coendou*, Landry (1957: 15) stated, "The teeth occlude on one side at a time, the entire lower jaw pivoting around the condyle on the opposite side. Thus if the stroke begins on the right side the jaw pivots around the left condyle, grinding the right cheek teeth together as

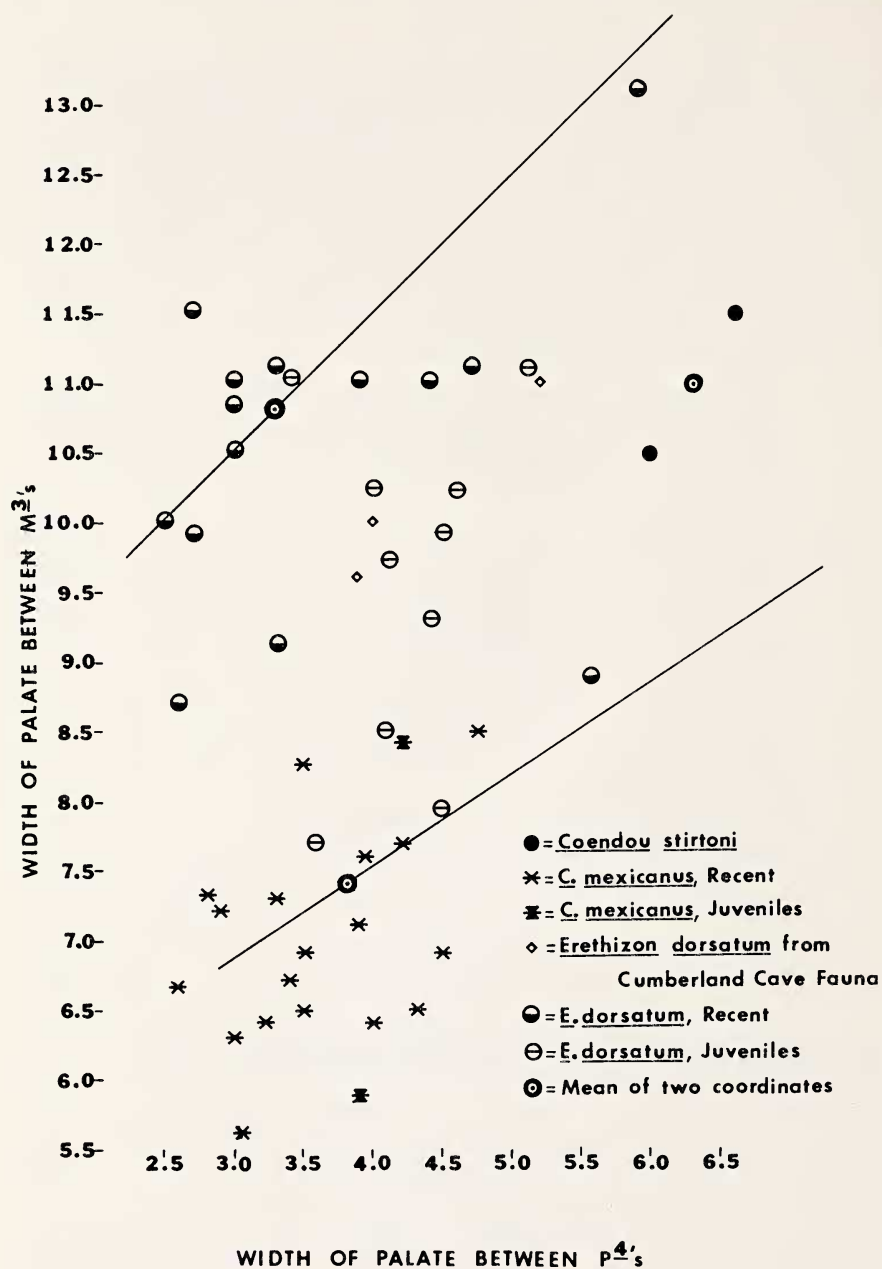


Figure 6. Scatter diagram and calculated reduced major axes (diagonal lines) for adults of *Erethizon dorsatum* and *Coendou mexicanus*. See Figure 4 for additional details.

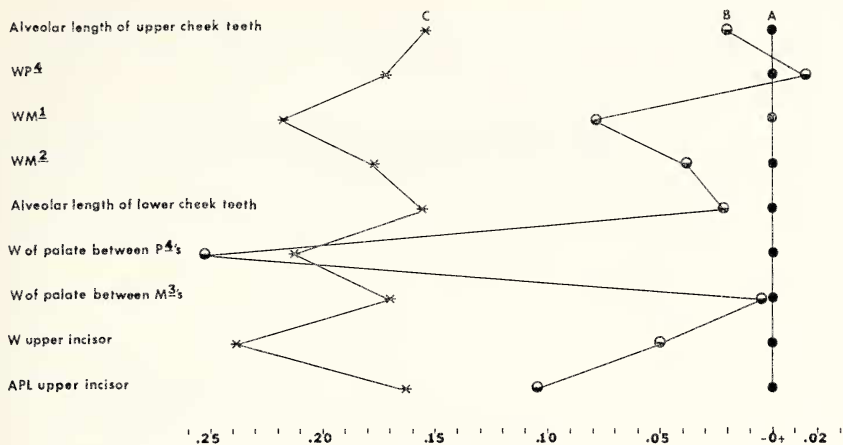


Figure 7. Ratio diagrams modified from Simpson *et al* (1960), comparing several cranial dimensions of *Coendou stirtoni* n. sp. (A), with *Erethizon dorsatum* (B), and *Coendou mexicanus* (C). The logs of the means of the dimensions of *C. stirtoni* are assumed to be zero, while the differences between the log of the mean in the latter species (standard) and species being compared are plotted on the positive (+) or negative (—) sides of the zero line.

the right condyle slides forward in the glenoid fossa." In *Erethizon* mastication occurs in a similar manner, but since the teeth in adults of the latter genus converge markedly anteriad, each of the masticatory strokes more closely parallels the longitudinal axis of the tooth row than in *Coendou*, where the tooth rows are subparallel. From the latter it can be inferred that adult *Erethizon* have a more efficient chewing mechanism than either *Coendou* or juvenile *Erethizon*.

Hibbard and Mooser (1963: 247-248) in referring a mandible from the Late Pleistocene (Hibbard *in litt.*) of Aguascalientes, Mexico, to *Erethizon*, noted that their specimen resembled the mandibles in *Erethizon*, except that: "The fossa on the lateral surface and posterior border of the coronoid process for the insertion of *M. masseter medialis*, *pars posterior* is slightly deeper than observed in the Recent specimens." and "The base of the coronoid process of the fossil does not ascend as vertically as in Recent specimens and therefore makes it possible to see the crowns of the teeth in lateral view." The scratches on the enamel of the occlusal surface of the cheek teeth in this specimen, and the projection of the longitudinal axis of the mandibular cheek teeth, are as in *Coendou* (Fig. 8). This indicates that the specimen (an adult) probably had a masticatory apparatus as in *Coendou* and juvenile *Erethizon*.

The base of the ascending ramus in the mandible described by Wilson (1935) as *Erethizon brachynathum* indicates that it probably sloped posteriad, and the anterior end of the fossa below the coronoid process suggests a condi-

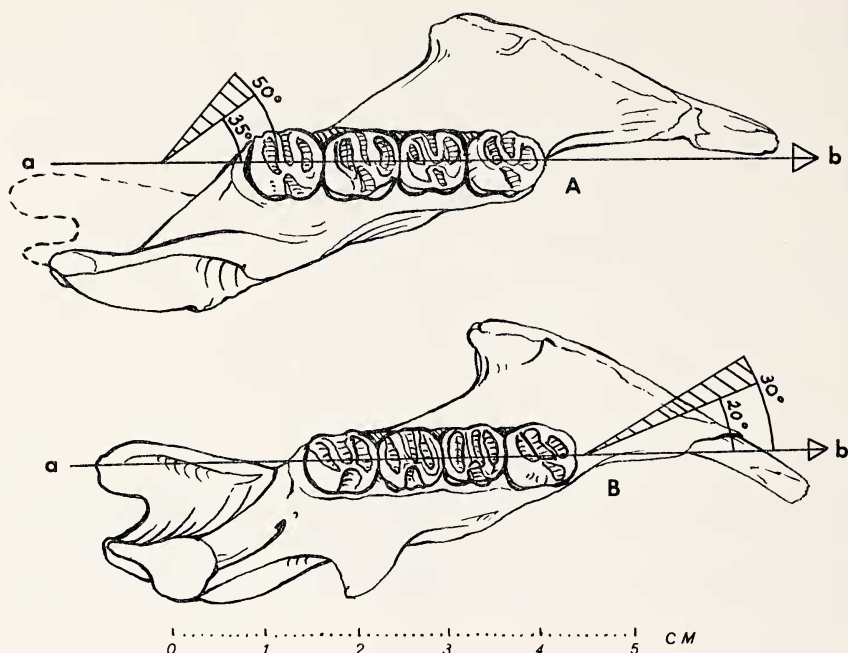


Figure 8. Dorsal views of the mandibles of *Coendou* from Aguascalientes, Mexico, UMM V47106 (A), and *Erethizon dorsatum*, USNM 90476 (B). Lines a-b bisect the cheek teeth longitudinally and project as shown by the arrows. The orientation of the scratches on the enamel of the occlusal surfaces of the cheek teeth is indicated by cross-hatching. See text for additional explanation.

tion essentially as in *Coendou*. The orientation of the scratches on the enamel of the cheek teeth of this specimen has not been determined.

In *E. brachignathum* Wilson, the Aguascalientes specimen of Hibbard and Mooser, and the maxillaries of *C. stirtoni*, the cheek teeth closely resemble those in living *Erethizon*. It is difficult to compare the structure of the cheek teeth of living *Coendou* with the above specimens or with those in living *Erethizon*, since the cheek teeth in living *Coendou* are markedly smaller in size, and there is great variability in the cheek-tooth structure of all these forms. The differences in masticatory function between *Coendou* and *Erethizon* are clearcut and seem, consequently, to be of greater importance than dentition in characterizing these two genera.

On functional grounds, then, it seems reasonable to refer tentatively *Erethizon brachignathum* Wilson to ?*Coendou brachignathum* (Wilson), and to refer the specimen from Aguascalientes described by Hibbard and Mooser (1963) to *Coendou*.

The pedomorphic nature of the structures relating to mastication in *Erethizon* strongly suggests that the condition found in adults of *Coendou* and in juveniles of *Erethizon* are primitive and presumably functionally less efficient than the condition found in adult *Erethizon*. Thus, it would seem that *Coendou* is the structural ancestor of *Erethizon*, and that the living species of *Coendou* either are relicts adapted to a narrow niche in the rain forests, or that both genera descended from an unknown, common ancestor in South America. Unfortunately, a fossil record of prehensile-tailed *Coendou* is unknown.

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TABLE 1

Measurements in millimeters of skull parts in *Coendou stirtoni* n. sp.

	LACM 17633	LACM 6136	LACM 6210A	LACM 6210
	(Type specimen)			
Breadth of rostrum				
lateral to incisors	—	17.6	—	—
Alveolar length of upper				
cheek-tooth series	27.7	25.9	—	—
Length of upper diastema				
from posterior surface of	—	39.2	—	—
incisor to P ⁴				
Width of crown on P ⁴	8.4	—	—	—
Width of crown on M ¹	8.4	—	—	—
Width of crown on M ²	7.8	—	—	—
Alveolar length of lower				
cheek-tooth series	—	—	30.7	—
Depth of mandible				
below M ₂	—	17.7	15.8	16.7
Breadth of palate				
between alveoli of P ⁴ 's	6.6	6.0	—	—
Breadth of palate				
between alveoli of M ³ 's	11.5	10.5	—	—
Width of upper incisor	—	4.8	—	—
Anteroposterior thickness				
of upper incisor	—	6.1	—	—

TABLE 2

Measurements in millimeters of skeletal parts in *Coendou stirtoni* n. sp.

	LACM 6136	LACM 4325
Humerus: distance from medial to lateral epicondyle.	—	28.2
Ulna: from proximal surface of articular facet of humerus to tip of olecranon process.	—	11.5
Radius: proximal head:		
Anteroposterior width	12.8	—
Transverse width	8.2	—
Femur: from mediolateral base of third trochanter to proximal tip of greater trochanter.	—	35.3
Anteroposterior width of head	21.5	—
Astragalus:		
width across trochlea	—	16.6
greatest anteroposterior length of lateral trochlea	—	15.2
width of distal articular head	—	8.6
Calcaneus:		
greatest anteroposterior length	—	34.5
greatest width	—	20.1
Cuboideum: from groove of <i>M. peroneus longus</i> to lateral margin of antiplantar surface	—	7.2